Case 3492

Heliconius tristero Brower, 1996 and Heliconius melpomene mocoa Brower, 1996 (Lepidoptera, NYMPHALIDAE): proposed conservation by suppression of Heliconius melpomene bellula Brown, 1979

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Abstract. The purpose of this application, under Articles 23.9.3 and 81.2.3 of the Code, is to conserve the species-group names Heliconius tristero Brower, 1996 and Heliconius melpomene mocoa Brower, 1996 (Lepidoptera: NYMPHALIDAE) for mimetic butterflies from the Putumayo region of southeastern Colombia by suppressing the senior name Heliconius melpomene bellula Brown, 1979. The authorship of this name is convoluted, bellula having been originally proposed as an unavailable quadrinomen and made available by Brown (1979). More significantly, because the implied holotype of Heliconius melpomene bellula Brown, 1979 does not belong taxonomically to the species whose oldest available name is Heliconius melpomene (Linnaeus, 1764), H. melpomene bellula Brown, 1979 is not a subjective synonym of H. melpomene (Linnaeus, 1764). Strict application of the Code would synonymise H. tristero Brower, 1996 with H. bellula Brown, 1979 and retain H. melpomene mocoa Brower, 1996 as a valid name. That action would reverse the current application of nomenclature for these taxa as published in numerous recent papers and result in significant confusion. Furthermore, given current disagreement among authors as to the taxonomic status of the specimen associated with the description of the name bellula, future nomenclatural instability is likely if the name is maintained. It is therefore proposed that the name Heliconius tristero be conserved and the name Heliconius bellula be suppressed.

Keywords. Nomenclature; taxonomy; Insecta; Lepidoptera; NYMPHALIDAE; Heliconius; Heliconius tristero; Heliconius melpomene mocoa; Heliconius melpomene bellula; butterflies; Colombia.

1. Stichel (1923) described a single specimen of Heliconius amaryllis amaryllis C. & R. Felder, 1862, with the name Heliconius amaryllis amaryllis Forma bellula from the vicinity of Mocoa in the upper Putumayo region of southeastern Colombia. Heliconius amaryllis is currently viewed as a geographical race or subspecies of Heliconius melpomene (Linnaeus, 1758) (cf. Ackery & Smiles, 1976; Lamas, 2004), occurring in the Huallaga Valley of northeastern Peru (Brown, 1979; Sheppard et al., 1985; Mallet & Barton, 1989). As a quadrinomen, the name Heliconius amaryllis amaryllis Forma bellula Stichel, 1923 is infrasubspecific and unavailable (Articles 10.2, 45.5 of the Code – Infrasubspecific names), and cannot be made available from its original publication by the regulations in any other Article of the Code, except by

a Commission's ruling (Article 45.5.1 of the Code). The provisions of Article 45.6 are not relevant in this case as they deal only with names following a binomen, while 'bellula' is following a trinomen.

- 2. Lamas (1998) asserted that under Articles 10c, 23j, 50c of the 3rd Edition of the Code (1985), Turner (1971) made available and became author of the name *Heliconius melpomene bellula*, based on his listing of the name 'bellula (?)' as a geographical race of *Heliconius melpomene* in a figure legend. However, Turner (1971) did not mention the name bellula anywhere else in the book chapter, and his listing of the name in the figure legend provided neither a description of the taxon (Article 13.ai), nor citation of a previous author's description (or even indication of Stichel as the author) (Article 13aii). Therefore, Turner's use of the name does not satisfy the criteria of availability stated in Article 13.1 (13a of the 1985 Code), and *Heliconius melpomene bellula* Turner, 1971 is a nomen nudum.
- 3. Brown (1979, Appendix 3, p. 117) made available and became the author of the name *Heliconius melpomene bellula* by treating it as a subspecies of *Heliconius melpomene* and citing Stichel (1923) (Articles 10.2, 13.1.2, 45.5.1, 50.3.1 of the Code Authorship of an infrasubspecific name), which by implication made Stichel's original specimen the holotype of the new nominal taxon (Articles 72.5.6, 73.1.2 of the Code Eligibility as name-bearing types). Subsequent authors (e.g. Sheppard et al., 1985; Mallet, 1993; Holzinger & Holzinger, 1994; Brower, 1996b) applied the name to the geographical race of *H. melpomene* from southeastern Colombia, and followed Brown (1979) in attributing authorship to Stichel (1923). The specimen described by Stichel (1923) became the holotype of *H. melpomene bellula* Brown, 1979 by monotypy (Article 73.1.2).
- 4. Brower (1996a) discovered based on mitochondrial DNA sequences that the then-current taxonomic concept of 'Heliconius melpomene bellula' comprised two taxa a subspecies of H. melpomene and a relative of the clade comprising Heliconius cydno Doubleday, 1847, H. heurippa Hewitson, [1854] and H. timareta Hewitson, 1867. Brower described and illustrated the former as H. melpomene mocoa and the latter as Heliconius tristero, and also examined and illustrated the holotype of Brown's bellula (= Stichel's single specimen). There is some suggestion that H. tristero was among the first species to be discovered and diagnosed by a combination of morphological features and DNA sequences. Brower pointed out two salient features of the Stichel specimen: that its genitalia imply it is related to the cydno group of species, and that its wing-pattern markings suggest that it is a hybrid backcross between H. tristero and another member of the cydno group. This interpretation is supported by the observation that Stichel (1923) first diagnosed the 'typical' form of H. amaryllis amaryllis Felder and then described Forma bellula as a variant of it with yellow spots on the forewings (see Brower, 2000).
- 5. Lamas (1998) published a critique of Brower's (1996a) taxonomic determinations, citing the Glossary of the 1985 Code 'the progeny of two individuals belonging to different subspecies of the same species are not hybrids') to argue that the name bellula could not be denied validity under Article 23h on the basis of its putative hybrid origin. Lamas synonymised *H. melpomene mocoa* Brower, 1996 with *H. melpomene bellula*, the species he attributed to Turner, 1971. Lamas repeated this synonymy in his widely-used checklist of Neotropical butterflies (Lamas, 2004) (see 2 and 3 above for a revised view on authorship and typification).

- 6. Brower (2000) published a response to Lamas (1998), again pointing out that Stichel's specimen, the holotype of H. melpomene bellula Brown, 1979, was not taxonomically an example of H. melpomene. Thus, Lamas' (1998) synonymy was incorrect. Lamas (1998) rejected Brower's (1996a) hypothesis of a hybrid origin of Stichel's specimen because no other relatives of H. tristero were then known from the vicinity of Mocoa. However, there is now evidence for additional cryptic cydno group taxa masquerading as other melpomene races in adjacent regions both north and south of Mocoa (Giraldo et al., 2008; Jiggins et al., unpublished data) that could provide alleles resulting in the putative hybrid wing-pattern elements observed in Stichel's specimen of bellula. Brower (2000) presented formal synonymies of the names mocoa and bellula and also addressed the taxonomic status of the bellula specimen as a 'hybrid'. Of course, given its age, the morphological attributes of this specimen cannot be corroborated by evidence from DNA, as have the taxonomic identities of the types of the names described by Brower (1996a). Note that although the name bellula Brown, 1979 would be excluded from zoological nomenclature under Article 1.3.3 if its holotype were deemed taxonomically to be a hybrid, the argument presented in this petition assumes that the name is available.
- 7. Subsequent authors (Brower & Egan, 1997; Mallet et al., 1998, 2007; Shaw, 1998; Penz, 1999; Brower, 2002, 2006; Gilbert, 2003; Lamas, 2004; Bull et al., 2006; Beltrán et al., 2007; Kronforst et al., 2007; Giraldo et al., 2008; Jiggins, 2008; Mallet, 2009) as well as numerous websites have universally employed the name *H. tristero* Brower, 1996 to refer to the relative of the *cydno* group, and *H. melpomene bellula* Turner, 1971 or *H. melpomene mocoa* Brower, 1996 for the subspecies of *H. melpomene*. This species complex is the subject of intense research due to the hypothesis of 'hybrid speciation' (cf. Mávarez et al., 2006), and the patterns of relationships among the taxa are already confused enough without a needless nomenclatural muddle. A list of 28 published and electronic examples of usage is held by the Commission Secretariat.
- 8. If the provisions of the Code are followed and the name bellula is available, then Heliconius tristero Brower, 1996 is a junior subjective synonym of Heliconius bellula Brown, 1979 (which is not taxonomically a member of the species Heliconius melpomene), while the name Heliconius melpomene mocoa Brower, 1996 is the only available name for the entity traditionally called H. melpomene bellula. This reversal of current usage is not satisfactory for the reasons indicated above.
- 9. The International Commission on Zoological Nomenclature is accordingly asked:
 - (1) to use its plenary power to suppress the name *bellula* Brown, 1979, as published in the trinomen *Heliconius melpomene bellula*, for the purposes of the Principle of Priority but not for those of the Principle of Homonymy;
 - (2) to place on the Official List of Specific Names in Zoology the following names: (a) tristero Brower, 1996, as published in the binomen *Heliconius tristero*;
 - (b) mocoa Brower, 1996, as published in the trinomen Heliconius melpomene mocoa;
 - (3) to place on the Official Index of Rejected and Invalid Specific Names in Zoology the name bellula Brown, 1979, as published in the trinomen Heliconius melpomene bellula (senior subjective synonym of Heliconius tristero Brower, 1996) and as suppressed in (1) above.

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References

- Ackery, P.R. & Smiles, R.L. 1976. An illustrated list of the type-specimens of the Heliconiinae (Lepidoptera: Nymphalidae) in the British Museum (Natural History). Bulletin of the British Museum (Natural History), Entomology, 32: 171–214.
- Beltrán, M., Jiggins, C.D., Brower, A.V.Z., Bermingham, E. & Mallet, J. 2007. Do pollen feeding, pupal-mating and larval gregariousness have a single origin in *Heliconius* butterflies? Inferences from multilocus DNA sequence data. *Biological Journal of the Linnean Society*, 92: 221–239.
- **Brower, A.V.Z.** 1996a. A new mimetic species of *Heliconius* (Lepidoptera: Nymphalidae), from southeastern Colombia, as revealed by cladistic analysis of mitochondrial DNA sequences. *Zoological Journal of the Linnean Society*, **116**: 317–332.
- **Brower, A.V.Z.** 1996b. Parallel race formation and the evolution of mimicry in *Heliconius* butterflies: a phylogenetic hypothesis from mitochondrial DNA sequences. *Evolution*, **50**: 195–221.
- Brower, A.V.Z. 2000. On the validity of *Heliconius tristero* and *Heliconius melpomene mocoa* Brower, with notes on species concepts in *Heliconius* Kluk (Lepidoptera: Nymphalidae). *Procedings of the Entomological Society of Washington*, **103**: 678–687.
- **Brower**, A.V.Z. 2002. Cladistics, populations and species in geographical space: the case of *Heliconius* butterflies. Pp. 5–15 in DeSalle, R., Giribet G. & Wheeler, W.C. (Eds.), *Molecular systematics and evolution: theory and practice*. Birkhäuser Verlag, Basel.
- **Brower**, A.V.Z. 2006. Problems with DNA barcodes for species delimitation: 'ten species' of *Astraptes fulgerator* reassessed (Lepidoptera: Hesperiidae). *Systematics and Biodiversity*, 4: 127–132.
- Brower, A.V.Z. & Egan, M.G. 1997. Cladistics of *Heliconius* butterflies and relatives (Nymphalidae: Heliconiiti): the phylogenetic position of *Eueides* based on sequences from mtDNA and a nuclear gene. *Proceedings of the Royal Society of London B*, **264**: 969–977.
- Brown, K.S., Jr. 1979. Ecologia Geográfica e Evolução nas Florestas Neotropicais. 265, 120 pp. Universidade Estadual de Campinas, Campinas, São Paulo, Brasil.
- Bull, V., Beltrán, M., Jiggins, C.D., McMillan, W.O., Bermingham, E. & Mallet, J. 2006. Polyphyly and gene flow between non-sibling *Heliconius* species. *BMC Biology*, 4:11, doi:10.1186/1741-7007-4-11. http://www.biomedcentral.com/1741-7007/4/11/.
- **Doubleday, E.** 1847. *The Genera of Diurnal Lepidoptera*, vol. 1. P. 103, plate 15 fig. 3. Longman, Brown, Green & Longmans, London.
- Felder, C. & Felder, R. 1862. Specimen faunae lepidopterologicae riparum fluminis Negro superioris in Brasilia septentrionali. Wiener Entomologische Monatschrift, 6: 65–80.
- Gilbert, L.E. 2003 Adaptive novelty through introgression in *Heliconius* wing patterns: evidence for a shared genetic 'tool box' from synthetic hybrid zones and a theory of diversification. Pp. 281–318 in Boggs, C.L., Watt, W.B. & Ehrlich, P.R. (Eds.), *Butterflies: Ecology and evolution taking flight*. University of Chicago Press, Chicago.
- Giraldo, N., Salazar, C. A., Jiggins, C. D., Bermingham, E. & Linares, M. 2008. Two sisters in the same dress: *Heliconius* cryptic species. *BMC Evolutionary Biology*, 8: doi:10.1186/1471-2148-8-324.
- **Hewitson, W.C.** [1854]. *Illustrations of new species of exotic butterflies, selected chiefly from the collections of W. Wilson Saunders and William C. Hewitson*, vol. 1, Heliconidae, plate 2, fig. 7. John Van Voorst, London.
- Hewitson, W.C. 1867. Descriptions of some new species of diurnal Lepidoptera. *Transactions of the Entomological Society of London*, (3)5: 561–566.
- Holzinger, H. & Holzinger, R. 1994. Heliconius and related genera. 328 pp. Sciences Nat., Venette, France.

- Jiggins, C.D. 2008. Ecological speciation in mimetic butterflies. BioScience, 58: 541-548.
- **Kronforst**, M.R., Salazar, C.A., Linares, M. & Gilbert, L.E. 2007. No genomic mosaicism in a putative hybrid butterfly species. *Proceedings of the Royal Society of London B*, **274**: 1255–1264.
- Lamas, G. 1998. Comentarios taxonómicos y nomenclaturales sobre Heliconiini neotropicales con designación de lectotipos y descripción de cuatro subespecies nuevas (Lepidoptera: Nymphalidae: Heliconiinae). Revista Peruana de Entomologia, 40: 111–125.
- Lamas, G. (Ed.). 2004. Atlas of Neotropical Lepidoptera. Checklist: Part 4A Hesperioidea Papilionoidea. 463 pp. Scientific Publishers/Association of Tropical Lepidoptera, Gaines-ville FL.
- Linnaeus, C. 1758. Systema Naturae, Ed. 10, vol. 1. 824 pp. Salvii, Holmiae.
- Mallet, J. 1993. Speciation, raciation and color pattern evolution in *Heliconius* butterflies: evidence from hybrid zones. Pp. 226–260 in Harrison, R.G. (Ed.), *Hybrid Zones and the Evolutionary Process*. Oxford University Press, Oxford.
- Mallet, J. 2009. Rapid speciation, hybridization and adaptive radiation in the *Heliconius melpomene* group. Pp. 177–194 in Butlin, R.K., Bridle, J.R. & Schluter, D. (Eds.), Speciation and Patterns of Diversity. Cambridge University Press, Cambridge.
- Mallet, J. & Barton, N.H. 1989. Strong natural selection in a warning-color hybrid zone. *Evolution*, 43: 421–431.
- Mallet, J., Beltran, M., Neukirchen, W. & Linares, M. 2007. Natural hybridization in heliconiine butterflies: the species boundary as a continuum. *BMC Evolutionary Biology*, 7: doi:10.1186/1471-2148-7-28.
- Mallet, J., McMillan, W.O. & Jiggins, C.D. 1998. Mimicry and warning color at the boundary between races and subspecies. Pp. 390–403 in Howard, D.J. & Berlocher, S.H. (Eds.), *Endless forms*. Oxford University Press, Oxford.
- Mavarez, J., Salazar, C.A., Bermingham, E., Salcedo, C., Jiggins, C.D. & Linares, M. 2006. Speciation by hybridization in *Heliconius* butterflies. *Nature*, **441**: 868–871, 11 supplementary pages.
- Penz, C.M. 1999. Higher level phylogeny for the passion-vine butterflies (Nymphalidae, Heliconiinae) based on early stage and adult morphology. Zoological Journal of the Linnean Society, 127: 277–344.
- Shaw, K. L. 1998. Species and the diversity of natural groups. Pp. 44–56 in Howard, D.J. & Berlocher, S.H. (Eds.), *Endless forms*. Oxford University Press, Oxford.
- Sheppard, P.M., Turner, J.R.G., Brown, K.S., Benson, W.W. & Singer, M.C. 1985. Genetics and the evolution of muellerian mimicry in *Heliconius* butterflies. *Philosophical Transactions of the Royal Society, London B*, 308: 433–613.
- Stichel, H. 1923. Kolombische Heliconius. (Lep., Rhop.). Deutsche Entomologische Zeitschrift, 1923: 260–270.
- **Turner, J.R.G.** 1971. Studies of Mullerian mimicry and its evolution in burnet moths and heliconid butterflies. Pp. 224–260 in Creed, R. (Ed.), *Ecological Genetics and Evolution*. Blackwell Scientific Publications, Oxford and Edinburgh.

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Comments on this case are invited for publication (subject to editing) in the *Bulletin*; they should be sent to the Executive Secretary, I.C.Z.N., c/o Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).